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Primate Resting Postures: Constraints by Foregut Fermentation?

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ABSTRACT

Although resting is one of the dominant behaviors of foregut-fermenting primates (i.e., colobines), their resting posture has rarely received attention. We hypothesize that colobines are more constrained in their resting position than hindgut-fermenting primates and that colobines assume a sitting resting position for specific reasons. To test this hypothesis, we followed two approaches. First, we observed resting positions in two captive individuals each of eight species and tested whether colobines rested in a sitting position more than other primates. Second, we collected literature data on free-ranging specimens of 31 species and again tested whether colobines rested in a sitting position more than other primates. Both approaches indicated that colobines spent more time in a sitting posture than other primates (73.0% vs. 23.2% in captivity and 83.0% vs. 60.9% in the wild, respectively). We hypothesize that the position of the digestive chamber and the necessity of frequently having to eructate digestion gases force colobines to take a sitting posture to avoid pressure on the thorax and respiratory organs.

Keywords: colobine, foregut fermenter, hindgut fermenter, positional behavior, sitting, sloths.

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Introduction

The way an animal rests can have an influence on digestive processes. This is most evident in ruminants, as they are characterized by a sorting mechanism in their forestomach that operates on the density of different-sized particles (Lechner-Doll et al. 1991), with smaller particles generally having a higher density than larger ones (Sutherland 1988; Clauss et al. 2009). Therefore, digesta are separated according to their buoyancy in the fluid-filled forestomach or reticulum (Clauss et al. 2010). Ruminants typically adopt a sternal resting posture (i.e., are in sternal recumbency; Balch 1955) and rarely lie on their side. The sternal resting position ensures a constant orientation of the reticulum relative to gravity, which facilitates particle sorting.

Positional behaviors, including posture and locomotion, have long been of interest to biological anthropologists (e.g., Napier 1967; Fleagle 1976; Mittermeier 1978; Gebo and Chapman 1995; Dunbar and Badam 1998; McGraw 1998*a*; Grueter et al. 2013). Most studies of primate positional behavior focus on locomotion, probably because it often provides valuable information in relation to factors directly related to fitness (e.g., predator avoidance and efficient access to their preferred food items and mates) and the interest of relating behavior to anatomy and fossil remains. While several studies have provided detailed information relating primate posture to the spatial distribution of food, foraging pattern, and activity budget (e.g., Gebo 1992; Gebo and Chapman 1995; McGraw 1998*b*), resting postures are usually only briefly described. However, resting behavior is one of the major components of primate activity budgets, particularly in leaf-eating species such as colobines (Fashing 2011; Kirkpatrick 2011), and is related to their daily feeding rhythm, thermoregulation, and/or vigilance behavior (Dasilva 1993; Matsuda et al. 2014*a*; Eustace et al. 2015).

If resting posture is linked to digestive physiology, through its influence on the rate and efficiency of particle separation, it should be apparent in foregut-fermenting arboreal folivores, such as the colobine monkeys. However, experiments with captive colobines with different-sized digesta markers suggest there is no particle-sorting mechanism (Schwarm et al. 2009). Even in the proboscis monkey (*Nasalis larvatus*) that ruminates (Matsuda et al. 2011), which should result in particularly

efficient digesta particle size reduction (Matsuda et al. 2014*b*), no sorting mechanism is evident when they are fed passage markers of different sizes (Matsuda et al. 2015). However, if other factors related to the presence of a forestomach constrain resting position, then we would expect a similar predominance of a sitting resting position in colobines.

The objective of our research was to test the hypothesis that there is a predominance of a sitting resting position in colobines. To meet our objective, we followed two different approaches. First, we observed resting positions in captive colobines and tested whether they spent more time resting in a sitting position than other primates observed in the same captive facility. Second, we evaluated literature data on the resting profiles of free-ranging animals and tested whether colobines spent more time resting in a sitting position than other primates. Typically, in comparative analyses, questions like these ones need to be addressed while accounting for the phylogenetic relationship of the investigated species (Garland et al. 2005; Nunn 2011). Such an approach is not possible in this case. Given the clear phylogenetic distinction between foregut-fermenting colobines and other primates, of which none has a forestomach, we are aware that any finding separating colobines from other primates cannot conclusively be ascribed to their digestive physiology but could be related to other factors peculiar to this phylogenetic group.

Material and Methods

Behavioral Observation

We studied eight primate species in the Singapore Zoo in January–February 2011: two foregut fermenters (*Nasalis larvatus* and *Colobus angolensis*) and six hindgut fermenters (*Erythrocebus patas, Macaca nigra, Alouatta caraya, Ateles fusciceps, Pongo abelii*, and *Pan troglodytes*; table 1). We collected behavioral data on two adults of each species during observation periods from 0900 to 1200 hours and from 1300 to 1730 hours. We observed each focal individual for 12 h, including 4 h of observation just after feeding time (20 min after food was given). Species were observed on a rotational basis with at least 2 h per individual within a group on each day. We collected 240 3-min focal samples for each individual, for a total of 192 h of observation of 16 individuals of eight different species. During the observations, we recorded the behavioral activities that were associated with each posture and the terrestriality of the focal animals (i.e., whether the individuals were on the ground or arboreal). The availability of subjects with a standardized age class limited the sample size. Additionally, the naturalistic design of the enclosures often prevented continuous observation of all individuals of a group, which would have been more appropriate than focal sampling.

Three behavioral categories (resting, moving, and feeding) were associated with seven postural states. Resting included all periods in which the subject was inactive. Moving included locomotion resulting in a change in spatial position; note that social grooming was included in this behavior category as grooming animals frequently changed positions—as they do in locomotion. Feeding included handling, masticating, or swallowing food items. Postural categories included (1) vertical sitting: the primate's body was 75°–90° perpendicular to the ground, corresponding to Hunt et al.'s (1996) "sit-in" and "sit-out" postures; (2) hunched sitting: the primate's body was approximately 60°–70° perpendicular to the ground, with the head tucked in between the knees or tilted down; (3) crouching on four legs: the primate's body was parallel to the ground and both the hind and forelimbs used to support the weight of the body were bent, corresponding to Hunt et al.'s (1996) "crouch" posture; (4) lying on belly: the primate's body was parallel to the ground, and limbs were not supporting the weight of the body (limbs were usually left dangling at the side of the body in midair or placed on branches/floor), corresponding to Hunt et al.'s (1996) "sprawl" posture; (5) lying on back: the primate's body was parallel to the ground, and limbs were sometimes raised in midair or rested on both sides on the ground, corresponding to Hunt et al.'s (1996) "back lie" posture; (6) lying on side: the primate's body was parallel to the ground and turned to one side, corresponding to Hunt et al.'s (1996) "lateral lie" posture; and (7) hanging: the primate's body was hanging sideways from branches via either the tail or limbs, and the body was parallel to the ground (usually it resembled a posture of lying on the belly or on the side without the physical support of a horizontal platform).

Linear mixed models were used to examine whether the proportion of time spent vertical sitting during resting across the individuals in each species was affected by body mass and digestive strategy (i.e., foregut/hindgut fermentation). We accounted for terrestriality in some models (divided into five categories, i.e., 1, ground utilization of <10% of 240 3-min samples; 2, <20%; 3, <30%; 4, <40%; 5, >50%) because sitting may be linked to the use of branches/climbing structures. The proportion of time spent in vertical sitting was logit transformed ($\log(p/1 - p)$) and treated as a normally distributed response variable. The other factors were treated as categorical explanatory variables, with the exception of body mass. In addition, a random intercept was determined for each species to account for the dependence of the response variable within a species. We examined a set of models with all possible combinations of the explanatory variables and ranked them by the corrected version of the Akaike information criterion (AIC) for small sample size, called AICc (Burnham and Anderson 2002). Analyses were performed in R, version 3.1.0 (R Development Core Team 2014), using the lmer function in the lme4 package, version 1.1-6 (Bates et al. 2013), and the dredge function in the MuMIn package, version 1.9.13 (Bartoń 2013). To compare the diversity of postures between the foregut/hindgut-fermenting species, the Shannon-Wiener index of diversity (H') using the observed frequency of the seven postures in each individual was calculated (Pielou 1966) and contrasted using the Mann-Whitney U-test. For all results, we reported means with standard deviation.

Literature Evaluation

Data on the proportion of time spent in a vertical sitting posture during resting were taken from the literature (table 2). If

Table 1: Behavioral observations of captive primates

Species, class, and sex	Body mass (kg)	Digestive strategy	Frequency of each observed activity (in 240 3-min samples)						Vertical sitting posture during resting (%)	Terrestriality	Diversity of posture (*H'*)
			Resting	(%)	Moving	(%)	Feeding	(%)			
Proboscis monkey (*Nasalis larvatus*):											
Adult male	21	F-F	188	78	26	11	26	11	76.1	2	.71
Subadult male	10	F-F	179	75	31	13	30	13	76.0	2	.81
Angolan colobus (*Colobus angolensis*):											
Adult male	10	F-F	200	83	14	6	26	11	76.0	1	.79
Adult female	7	F-F	195	81	23	10	22	9	64.1	1	1.01
Black-and-gold howler monkeys (*Alouatta caraya*):											
Adult male	11	H-F	199	83	19	8	22	9	11.1	1	1.48
Adult female	6	H-F	201	84	17	7	22	9	12.4	1	1.53
Brown-headed spider monkey (*Ateles fusciceps*):											
Adult male	9	H-F	205	85	19	8	16	7	17.1	1	1.64
Adult female	9	H-F	198	83	23	10	19	8	23.2	1	1.55
Crested macaque (*Macaca nigra*):											
Adult male	7	H-F	184	77	24	10	32	13	24.5	5	.65
Adult female	5	H-F	183	76	36	15	21	9	34.4	5	1.17
Patas monkey (*Erythrocebus patas*):											
Adult male	13	H-F	194	81	30	13	16	7	28.9	5	1.64
Adult female	7	H-F	187	78	37	15	16	7	32.1	5	1.40
Sumatran orangutan (*Pongo abelii*):											
Adult male	60	H-F	193	80	23	10	24	10	26.9	4	1.00
Adult female	47	H-F	190	79	30	13	20	8	24.2	4	1.33
Chimpanzee (*Pan troglodytes*):											
Adult male	78	H-F	193	80	23	10	24	10	17.6	4	1.23
Adult female	38	H-F	203	85	16	7	21	9	25.6	4	1.27

Note. F-F = foregut fermenter; H-F = hindgut fermenter.

Table 2: Proportion of resting time spent by various primate species in a sitting posture from literature data on free-ranging individuals

Species	Digestive strategy	Diet type[a]	Sitting posture during resting (%)	Source for posture data
Piliocolobus tephrosceles	F-F	Folivorous	93.0	Gebo and Chapman 1995
Piliocolobus badius	F-F	Folivorous	80.4	McGraw 1998*b*
Colobus guereza	F-F	Folivorous	78.0	Gebo and Chapman 1995
Colobus polykomos	F-F	Folivorous	70.7	Dasilva 1993
Colobus polykomos	F-F	Folivorous	82.8	McGraw 1998*b*
Presbytis femoralis	F-F	Folivorous	94.0	Fleagle 1980
Procolobus verus	F-F	Folivorous	86.9	McGraw 1998*b*
Rhinopithecus bieti	F-F	Folivorous	74.0	Grueter et al. 2013
Trachypithecus delacouri	F-F	Folivorous	98.1	Workman and Schmitt 2011
Trachypithecus obscurus	F-F	Folivorous	76.0	Fleagle 1980
Alouatta caraya	H-F	Folivorous	35.0	Bicca-Marques and Calegaro-Marques 1998
Alouatta palliata	H-F	Folivorous	65.0	Mendel 1976
Alouatta seniculus	H-F	Folivorous	33.1	Schon 1984
Ateles geoffroyi	H-F	Frugivorous	38.5	Fontaine 1990
Ateles geoffroyi panamensis	H-F	Frugivorous	47.4	Mittermeier 1978
Ateles paniscus paniscus	H-F	Frugivorous	47.5	Mittermeier 1978
Cacajao calvus calvus	H-F	Frugivorous	66.7	Walker and Ayres 1996
Lophocebus albigena	H-F	Frugivorous	73.0	Gebo and Chapman 1995
Cercopithecus ascanius	H-F	Frugivorous	89.0	Gebo and Chapman 1995
Cercopithecus campbelli	H-F	Frugivorous	97.2	McGraw 1998*b*
Cercopithecus diana	H-F	Frugivorous	87.3	McGraw 1998*b*
Cercopithecus mitis	H-F	Generalist	57.0	Gebo and Chapman 1995
Cerocebus atys	H-F	Frugivorous	98.4	McGraw 1998*b*
Gorilla gorilla gorilla[b]	H-F	Generalist	52.7	Remis 1995
Hylobates agilis	H-F	Frugivorous	95.0	Fleagle 1980
Pan troglodytes schweinfurthii	H-F	Frugivorous	21.5	Hunt 1992
Pan troglodytes verus	H-F	Frugivorous	57.7	Doran 1993
Papio anubis	H-F	Generalist	81.7	Rose 1977
Pongo pygmaeus abelii	H-F	Frugivorous	59.4	Sugardjito and van Hooff 1986
Saimiri boliviensis	H-F	Frugivorous	49.3	Fontaine 1990
Symphalangus syndactylus	H-F	Frugivorous	87.0	Fleagle 1980
Varecia variegata variegate[c]	H-F	Frugivorous	34.9	Morland 1993

[a]Diet types from Mittermeier et al. (2013).
[b]Only arboreal resting postures were available.
[c]Percent was calculated as the average of values read from the graph.

the respective publication did not distinguish between vertical sitting and hunched sitting (as outlined above) but just reported "sitting," this value was used. Thus, 32 samples (31 different species/subspecies), including 10 samples (nine species) of foregut fermenters and 22 samples (22 species/subspecies) of hindgut-fermenting species, were available (table 2). The proportions of time spent sitting were compared between the foregut/hindgut-fermenting species using Mann-Whitney *U*-tests. Because available data on terrestriality and body mass were limited in the literature data collection, these factors were not considered. In primates, the proportion of the observed daytime spent resting typically increases with the proportion of leaves in the natural diet (Korstjens et al. 2010). Therefore, in order to test whether the results were influenced by the inclusion of different diet types in the data set, each species was allocated a diet type (folivore, frugivore, generalist) according to Mittermeier et al. (2013); again, an evaluation of models linking the proportion of time spent in vertical sitting to both diet type and digestive strategy was performed using the AICc as explained above.

Results

Resting Posture in Captive Primates

Resting was the most dominant behavior for all primate species, accounting for >75% of the time (table 1). Although all animals engaged in resting for most of the day, the proportion of time

spent in vertical sitting differed among species. The best-fit model (ΔAICc < 2) included only the factor digestive strategy (table 3). This demonstrates that foregut fermenters/colobines spent significantly more time in the vertical resting posture (73.05 $\pm$ 6.0%) than hindgut fermenters (23.2% $\pm$ 7.3%). The measure of relative variable importance (one of the multimodel inference outcomes; Burnham and Anderson 2002) also indicated strong evidence for the importance of this dichotomy: 0.98 for digestive strategy/phylogeny, 0.03 for terrestriality, and 0.15 for body mass (table 3). The mean diversity index (H') of postures in hindgut-fermenting species (1.32 $\pm$ 0.29) was significantly higher than that in foregut-fermenting species (0.83 $\pm$ 0.13; *U*-test: $Z = -2.30$, $P = 0.02$), suggesting that hindgut fermenters had more freedom to vary their resting postures.

Resting Posture in Free-Ranging Primates

The proportion of resting time spent in a sitting posture ranged from 21.5% to 98.1% in the primates considered in the literature review (mean = 69.0% $\pm$ 22.1%). The mean proportion of time spent sitting was significantly higher in foregut fermenters/colobines (83.4% $\pm$ 9.28%) than in hindgut fermenters (69.0% $\pm$ 22.1%; $Z = 2.236$, $P = 0.025$). Limiting the comparison to folivorous species only (which basically represents a comparison of colobines and howler monkeys) yields a similar difference (83.45% $\pm$ 9.3% vs. 44.4% $\pm$ 17.9%; $Z = 2.535$, $P = 0.011$). The best-fit model (ΔAICc = 0) included only the factor digestive strategy (table 4); however, the model without either digestive strategy or diet type was equally well supported (ΔAICc = 1.95). Models including diet type were less supported (table 4). The model including digestive strategy (1 = foregut fermentation, 2 = hindgut fermentation) and diet type (1 = folivory, 2 = generalist, 3 = frugivory) indicated that the time spend in a sitting posture was significantly higher in foregut fermenters ($a = -2.08$ [95% confidence interval (CI) -3.77, -0.40], $P = 0.022$) and not significantly higher in frugivorous species ($b = 1.25$ [95% CI -0.36, 2.87], $P = 0.140$).

Discussion

The results supported our hypothesis that foregut-fermenting primates are more constrained in their resting position than primates with other digestive strategies and that foregut fermenters in particular assume a vertical sitting resting position; they also indicate that diet type (folivory vs. frugivory) is of limited relevance in this question. Our study has important limitations in its ability to conclusively link a sitting resting posture to a physiological system, that is, foregut fermentation. Due to logistical reasons, only a few captive individuals were observed for a limited time. Therefore, a more comprehensive recording of resting positions from a larger number of specimens and species is desirable, also with respect to nonprimate, nonruminant mammalian foregut fermenters. Observations of captive individuals, as made in our study, should be expanded in terms of both the number of individuals included and the observation time; ideally, care should be taken to provide all species with the same complete set of resting opportunities to ensure that enclosure design does not favor a particular resting posture not typical for the species. With respect to data from free-ranging specimens, our analysis of available literature data need not necessarily yield the same results as comparisons between individual species (McGraw 1998*b*); in particular, our hypothesis does not suggest that noncolobine species sit less frequently but that foregut fermenters do not have the same freedom in choosing their resting position.

The strategy of foregut fermentation evolved only once in primates—in the colobine subfamily (Langer 1988). Therefore, any result that sets this group apart need not necessarily be related to their digestive strategy but may be associated with other factors. In particular, the clear phylogenetic separation of digestive strategies makes an evaluation by statistical procedures that account for the phylogenetic structure of the data set (Garland et al. 2005; Nunn 2011) impossible. However, a comparison with another group of arboreal foregut-fermenting folivores, the sloths (Clauss 2004), makes this interpretation more plausible. Assuming that a similar density-dependent particle-sorting mech-

Table 3: Summary of model selection for the observational data from captive specimens

Intercept	Digestive strategy	Terrestriality	Body mass	df	Log likelihood	AICc	ΔAICc	AICc weight
4.93	+			4	−.42	12.5	.00	.82
4.98	+		−3.70.E-03	5	−.01	16.0	3.54	.14
4.92	+	+		7	4.40	19.2	6.72	.03
4.05				3	−6.73	21.5	8.97	.01
4.22			−7.89.E-03	4	−5.16	21.9	9.47	.01
4.99	+	+	−8.38.E-03	8	5.89	24.8	12.32	.00
3.92		+		6	−4.92	31.2	18.69	.00
4.00		+	−8.49.E-03	7	−3.42	34.8	22.35	.00
	Summed AICc weight for predictor variables (the measure of relative variable importance)							
	.98	.03	.15					

Note. A plus sign indicates inclusion of the variable in the model. The bottom row shows the measure of relative variable importance (Burnham and Anderson 2002), which is calculated as the total sum of the AICc weight of all models in which the given predictor variable occurs (AICc = corrected version of the Akaike information criterion for small sample size). df = degree of freedom.

Table 4: Summary of model selection for the literature data from wild specimens

Intercept	Digestive strategy	Diet type	df	Log likelihood	AICc	ΔAICc	AICc weight
1.85	+		3	−53.2	113.3	.00	.60
1.12			2	−55.4	115.2	1.95	.23
1.85	+	+	5	−51.9	116.1	2.85	.14
1.37		+	4	−54.9	119.4	6.10	.03
	Summed AICc weight for predictor variables (the measure of relative variable importance)						
	.74	.17					

Note. A plus sign indicates inclusion of the variable in the model. The bottom row shows the measure of relative variable importance (Burnham and Anderson 2002), which is calculated as the total sum of the AICc weight of all models in which the given predictor variable occurs (AICc = corrected version of the Akaike information criterion for small sample size). df = degree of freedom.

anism exists in foregut-fermenting sloths (*Bradypus* and *Choloepus* spp.) as we have proposed for colobines, Clauss (2004) suggested that the typical sitting resting posture of these animals matched their digestive anatomy and could help facilitate particle sorting. The predominance of the sitting resting position in sloths was confirmed in the field study of Urbani and Bosque (2007).

Despite our findings, there is reason to question the existence of a particle-sorting mechanism in the forestomach of colobines. Experimental evidence from colobines indicates that small and large particles pass through their digestive tract in parallel (Schwarm et al. 2009; Matsuda et al. 2015), while they are retained differentially in true functional ruminants (Dittmann et al. 2015). Investigations of physical aspects of the forestomach contents of primates that would allow a comparison to other foregut fermenters (Clauss et al. 2009; Schwarm et al. 2013) have not been performed. In addition, a general peculiarity of primate digestive physiology makes such a separation mechanism less likely. Namely, a large number of digesta passage experiments performed with a number of primate species indicate that the fluid and the particulate digesta phase move in parallel (Müller et al. 2011; Matsuda et al. 2015). This makes the accumulation of fluid in any particular gut compartment less likely, which would be necessary for a separation mechanism based on buoyancy. Therefore, in contrast to what Clauss (2004) suggested for sloths, we suggest that a causative link between the resting posture and forestomach fermentation in arboreal folivores must be sought outside of a putative particle-sorting mechanism.

We propose that the larger chamber's fermentation may enforce a sitting position to avoid pressure on the thorax and its respiratory organs. Since colobines do not harbor higher amounts of digesta in their digestive tract than other primates (Chivers and Hladik 1980; Kay and Davies 1994), such reasoning should apply to all herbivorous primates with capacious guts and not only to the foregut fermenters; however, this is not the case. For example, howler monkeys (*Alouatta* spp.), known to consume a highly herbivorous diet during some periods (Milton 1978), have a hindgut fermentation chamber (Edwards and Ullrey 1999) of smaller volume than the forestomach of colobines (Chivers and Hladik 1980), infrequently engaged in a vertical posture in this study. Gorillas, with their extremely voluminous (yet unquantified) hindgut, also often rest in a nonsitting posture (Lukas et al. 2003).

The location of the fermentation chamber in the gastrointestinal tract may have an influence on whether it exerts pressure on the thorax. A voluminous hindgut chamber may more easily be allocated space in a bulging abdomen (Clauss et al. 2017), whereas a forestomach may be confined to the lower part of the ribcage. One peculiarity of colobines (with the evident exception of the proboscis monkeys with their bulging abdomens) is their slender appearance despite their voluminous forestomachs. This appearance led to the German term "Schlankaffen," or "slender monkeys," for this group (e.g., Kuhn 1964); it may well describe a condition of the digestive tract that cannot respond through abdominal bulging. To further investigate a relationship between the space allocated to organs in the thoracic and abdominal cavities, comparative measures of the resting respiratory rate in colobine and noncolobine primates would be useful. This would be similar to a study in ruminants (Mortolaa and Lanthier 2005). That study suggested that a voluminous forestomach reduces the space available for lung tissue in the thoracoabdominal cavity and that the reduction in lung tissue is compensated for by an increased breathing frequency.

Another reason for the maintenance of a resting sitting position in foregut-fermenting primates could be the necessity to frequently eructate digestion gases. In ruminants, an increase in intraruminal pressure triggers eructation contractions (Weiss 1953), and eructation occurs 0.4–0.8 times per minute (Dziuk et al. 1963; Dziuk 1965; Dziuk and McCauley 1965). In colobines, quantitative studies on eructation are lacking, to our knowledge, but descriptions of captive animals report frequent eructations that can be easily observed (Kuhn 1964; Hollihn 1971). Using results from in vitro fermentation assays with forestomach content of (captive) *Procolobus badius* and *Presbytis cristatus*, Kuhn (1964) calculated a gas production rate of 300–1000 mL/h—a relevant amount that needs to be released. The relevance of unimpeded eructation from the forestomach is also emphasized by numerous reports of health problems in captive colobines due to a condition called "frothy bloat," in which gastric distension occurs because of a difficulty of releasing fermentation gases (Osman Hill 1964; Collins and Roberts 1978; Ruempler 1998); Hollihn (1973, p. 187) called this condition "the most common digestive disorder of

captive colobids and frequently the cause of death." Given that gas from the forestomach (in contrast to gas formed in the hindgut) is unlikely to be passed on toward the anus, and assuming a similar frequency in the need to eructate in foregut-fermenting as in ruminants, the necessity of gas eructation may constrain foregut fermenters to a sitting resting position.

Ischial callosities represent another characteristic with a clear phylogenetic signal among primates. They are considered adaptations to the frequent use of a sitting posture (Washburn 1957; Rose 1974*a*, 1974*b*; Vilensky 1978; McGraw and Sciulli 2011). The question of whether this refers to the sitting posture as a preferred resting position, or as the typical feeding position, remains unanswered; note that these views are not mutually exclusive. Recent evidence supports the interpretation that these callosities are particular adaptations to feeding on terminal branches (McGraw and Sciulli 2011). Ischial callosities are mainly limited to cercopithecidae and hylobatidae (Rose 1974*a*), and, therefore, they are present both in foregut fermenters (Colobinae) and in hindgut-fermenting Old World primates. If our findings are corroborated in further studies, this would indicate that the callosities may represent adaptations to a feeding behavior rather than to a resting behavior.

The relevance of resting postures could be investigated in species that can adopt a variety of such postures. For example, it could be hypothesized that a lying posture is related to a state of reduced vigilance and higher muscle relaxation. In this respect, comparisons of resting postures between free-ranging and captive individuals of species would be interesting, because of the reduced vigilance in captivity (van Schaik et al. 2016). Resting postures, in particular sleeping postures, have been linked to the selection of sleeping sites on thin branches out of the easy reach of predators (Washburn 1957; Rose 1974*a*, 1974*b*), and the absence or presence of predators may therefore influence the postures adopted—in light of the finding that within the human species, sleeping posture is related to parameters describing sleep quality (e.g., Nojiri et al. 2014). Hypothetical benefits of a lying posture, such as for the quality of sleep, could then represent an additional constraint exerted by the digestive strategy of foregut fermentation.

In addition, future studies should assess not only how differences between species but also how environmental factors, such as weather conditions, the characteristics of the support structures provided, or even the forest/habitat type, impact resting postures of primates. Resting postures are related to thermoregulation in some primate species including colobines (Stelzner and Hausfater 1986; Dasilva 1993; Bicca-Marques and Calegaro-Marques 1998; Anderson 2000); thus, some primates spend more time sitting/hunching depending on air temperature. In addition, for example, harsh habitats like limestone kerst appear to influence primate locomotion and posture patterns (e.g., Workman and Schmitt 2011), indicating that comprehensive analyses should be performed for further understanding of the relationship between posture and physiological systems in wild primates. However, we have to note that captivity generally reduces the influence of such potential environmental factors. Therefore, posture behaviors among captive specimens of different species may produce clearer results than in the wild. Thus, accumulating a catalogue of resting postures in a large number of captive primate species appears to be an appealing future prospect.

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